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FUNCTIONAL COMPOSITION OF MID-STREAM GRAVEL BAR VEGETATION (MIDDLE DRAVA RIVER, NE SLOVENIA)

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ABSTRACT

In the present study we sampled vegetation, plant functional traits and environmental properties to investigate the functional composition of gravel bar vegetation along the middle Drava River in Slovenia in relation to various abiotic controls. Our analysis of the species-traits data resulted in six plant functional types (FTs) which may coexist within gravel bar plant communities. Conditions of intermediate fertility and disturbance (areas with coarse gravel sediments, from low to higher micro-elevations) promote coexistence of a greater diversity of species and FTs. More fertile and moist conditions on areas with fine silt and sand sediments increased the dominance by tall plants with more competitive strategies, thereby leading to lower species richness and lower number of FTs. This study shows that gravel bars form a highly significant landscape element in terms of maintaining higher functional diversity of river ecosystem.

Key words: Plant functional traits, functional diversity, river ecosystems, plant diversity, flood disturbance, Natura 2000.

COMPOSIZIONE FUNZIONALE DELLA VEGETAZIONE DELLE BARRE GHIAIOSE NEL FLUSSO INTERMEDIO (FIUME DRAVA CENTRALE, SLOVENIA NORD-ORIENTALE)

SINTESI

Nel presente studio gli autori hanno campionato la vegetazione, le caratteristiche funzionali delle piante e le variabili ambientali al fine di indagare la composizione funzionale della vegetazione delle barre ghiaiose nella parte centrale del fiume Drava in Slovenia. L'analisi dei dati specie-tratti ha portato al risultato di sei tipi funzionali di piante (FTs), che possono coesistere all'interno delle comunità vegetali delle barre ghiaiose. Le condizioni di fertilità intermedia e di disturbo (aree con sedimenti ghiaiosi grossolani) possono promuovere la coesistenza di una maggiore diversità di specie e FTs. Condizioni più fertili e umide in zone con sedimenti fini di limo e sabbia aumentato il predominio di piante alte con strategie più competitive, e portano ad una diminuzione della ricchezza di specie e del numero di FTs. Lo studio dimostra che le barre ghiaiose costituiscono un elemento paesaggistico molto significativo in termini di mantenimento di una diversità funzionale elevata dell'ecosistema fluviale.

Parole chiave: caratteri funzionali della pianta, diversità funzionale, ecosistemi fluviali, diversità vegetale, disturbi da inondazioni, Natura 2000.

INTRODUCTION

The maintenance of Life on Earth depends on an efficient ecosystem functioning (Laureto *et al.*, 2015). Ecosystem functions represent processes that regulate the flux of energy and matter through the environment (e.g. nutrient cycling, storage and recycling of organic matter, erosion control, and decomposition) and several aspects of human well-being depend on benefits provided by ecosystems (the so-called ecosystem services, Millenium Ecosystem Assessment, 2005). Extensive declines in biodiversity at both global and local level have motivated many scientific studies demonstrating how loss and changes in biodiversity may affect ecosystem functioning and ecosystem services (ES) (Tilman *et al.*, 1997; Díaz *et al.,* 2006; Villeger *et al*., 2008).

Plant diversity is an important driver of ecosystem functioning (Villeger *et al.,* 2008) which contributes significantly to the delivery of ES (Lavorel & Grigulis, 2012). Particularly, functional components of diversity strongly determine different ecosystems properties and there is a growing consensus, that functional diversity, rather than species diversity (species number), is the component of biodiversity most relevant to ES (Hooper *et al.,* 2002; Bellwood *et al.,* 2004; Díaz *et al*., 2006; Wright *et al*., 2006; de Bello *et al*., 2010).

Functional diversity can have different definitions (Díaz & Cabido, 2001; Ricotta & Moretti, 2011) and can be quantified using a variety of indices (Villeger *et al*., 2008). Widely adopted definition for functional diversity is "the value and range of functional traits of the organisms present in a given ecosystem" (Díaz & Cabido, 2001). With functional diversity indices we can identify patterns of community structure reflecting complementarity of resource use or trait redundancy (Lavorel *et al*., 2011). One commonly used technique for measuring functional diversity consist of clustering species with shared taxonomic, physiological and morphological traits into functional groups (Wright et al., 2006). These alternative classes are referred to as plant functional types (PFTs) (Gitay & Noble, 1997; Pipenbaher *et al*., 2008), assuming that groups with similar traits differ in their response to and effect on resources (Lavorel & Garnier, 2002). Functional diversity has been seen as the key to predicting the stability, invisibility, and resource capture, nutrient cycling and productivity of communities. It had been suggested that ecosystems with a greater diversity of functional traits, i.e. higher functional diversity, will operate more efficiently (Tilman *et al*., 1997). The number of functional groups can be used as an approximation of functional diversity in an ecosystem (Wright *et al*., 2006).

Gravel bars are a typical feature of the braided gravel-bed rivers that were once widespread in temperate piedmont and mountain-valley areas (Tockner *et al.,* 2006). Because of their aquatic-terrestrial ecotone environment, are highly dynamic, with the potential to support high biodiversity and a range of environmental processes (Sadler *et al.,* 2004; Zeng *et al.,* 2015). The vegetation dynamics on river gravel bars is an indicator of the health of the river-floodplain ecosystem. Today, however, owing to anthropogenic modification - flood control engineering, canalization and gravel extraction - most gravel-bed rivers bear little resemblance to their highly dynamic natural state (Trockner *at al.,* 2006; Schnauder & Moggridge, 2009). Consequently, braided rivers are among the most endangered ecosystems (Sadler *et al*., 2004), and gravel bars are recognized as one of the most endangered landscape elements worldwide (Trockner *et al.,* 2006; Zeng *et al.,* 2015).

Patterns of plant species distribution and diversity on gravel bars are shaped according to a multitude of environmental gradients, including elevation above the water line, frequency, depth and duration of flooding, and various soil properties, in particular, the particle size and moisture content of sediment (Ellenberg, 1988; Prach, 1994; Prach *et al.,* 2014). Floods act as the main disturbing factor (Gilvear & Willby, 2006; Prach *et al*., 2014) and are fundamental in creating and maintaining environments that comprise habitats in various successional stages of different age, each with its own distinct vegetation community (Gray & Harding, 2007). An understanding of the relative roles of the various environmental controls on gravel bar vegetation forms the prerequisite for developing sustainable management schemes (Ward *et al.,* 2001) and for successful restoration (Tockner *et al.,* 2006; O´Donnell *et al.,* 2015).

There is a little published information on the complex relationship between environmental conditions and biodiversity of gravel bars (Gilvear & Willby, 2006; Zeng *et al.,* 2015) and the knowledge about the correlations of the environmental factors with the gravel bars vegetation pattern was expressed only in terms of floristic composition (Gilvear & Willby, 2006; Eremiášová & Skokanová, 2014). However, the investigations of functional trait diversity of gravel bar vegetation, considered as the overall difference among species in a plant community in terms of their traits, remains to be carried out. There is no knowledge about how functional diversity of gravel bar plant communities changes in response to combined environmental gradients such as micro-elevation above the water line and texture of the substrate, making it difficult to project the future structure and function of this ecosystem.

With a length of 750 km and an average discharge of 550 m^3/s at its mouth, the Drava River is one of the most important tributaries of the Danube River (Takács & Kern, 2015). It originates in the Alpine Mountains and joins the Danube at the edge of the Pannonian lowland. In the middle Drava River system in Slovenia, where this study was conducted, natural disturbances are still allowed to occur. It forms part of the network of NATURA 2000 sites. Therefore, it can serve as model system for study the complex relationship between environmental conditions and biodiversity of rivers and their landscape elements (Tockner *et al*., 2006). Such studies are needed for river restoration and management purposes (Zeng *et al.,* 2015).

In this study, we sampled vegetation, plant functional traits and environmental properties to investigate the functional composition of gravel bar vegetation along the middle Drava River in Slovenia in relation to various abiotic controls. Specifically, we focused on the following questions: (1) How many different plant functional types could be defined on the studied gravel bars?; (2) How is the plant functional composition of river gravel bar vegetation related to morphological and sedimentological properties?

MATERIALS AND METHODS

Study site

We studied vegetation on gravel bars alongside the middle Drava River (northeastern Slovenia, southern central Europe). Our study area was located in its middle stream between Ptuj and the Croatian border near Ormož: a belt about 15 km long between 46°25′ N and 15°52′ E, 16°09′ E, at ca. 200 m above sea level (Fig. 1). According to Köppen's classification (Köppen, 1923), the climate of the study area belongs to the climatic type Cfb (moderately warm, rainy climate without a dry period). The long-term mean maximum temperature in the warmest month (July) is 19.6 °C and the mean minimum temperature in the coldest month (January) is -1.5 °C. The average annual precipitation is between 900 mm and 1000 mm. The precipitation is spread rather evenly through the year, with a maximum in summer (July and August) and a minimum in winter (January, February) (Žiberna, 2000).

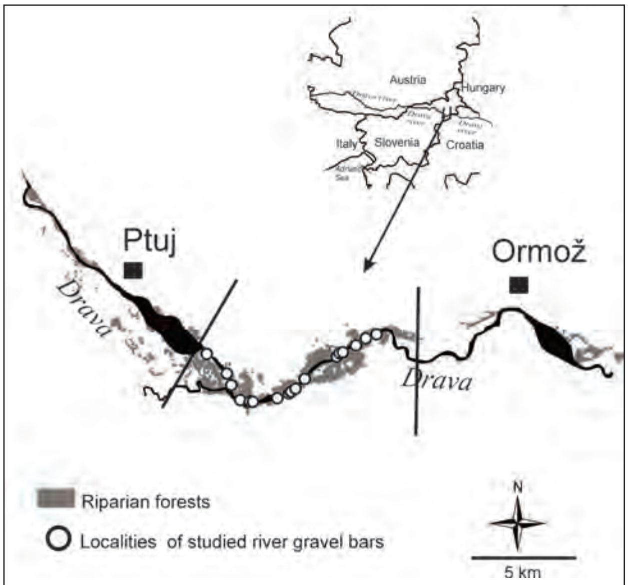


Fig. 1: Map of Slovenia and neighbouring regions. The more detailed map shows the position of studied gravel bars (N=17) along the middle Drava River in Slovenia.
Sl. 1: Prikaz območja Slovenije in sosednjih držav. Karta v večjem merilu prikazuje lokacije prodišč (N=17) vzdolž srednjega toka reke Drave v Sloveniji.

Data sampling

In April 2011 the total study area along this stretch of river was scanned using field observation with aerial photos. For data sampling, we selected only those gravel bars obviously undisturbed by human activities. Within these bars, we distinguished particular vegetation stages that were uniform in vegetation cover and located at the same height above the water line in the river at the time. We sampled differently aged stages of succession from bare deposits with sparse herb vegetation, to well-developed stands of *Salix* species. In our study, we examined seventeen (17) mid-channel river bars (Fig. 1). *We randomly sampl*ed multiple sites (min. 4 and max. 13 plots per bar) across each of 17 *gravel bar* systems; in total, 143 sampling plots were surveyed.

The species composition data of the gravel bar vegetation were collected between May and September 2011. Species composition was recorded in 143 plot relevés, each measuring 5 x 5 m. In each 25m^2 plot, vascular plants were sampled using, a seven-point cover-abundance scale according to Braun-Blanquet (1964). All plant species occurring in only one relevé were removed, to exclude casual occurrences from the analyses. In each plot, species richness was noted as the number of species recorded, and vegetation cover was estimated visually as the percentage of ground *covered* by *vegetation*. The rough grouping to species occurring in grassland communities, woodland and shrubland communities and disturbed habitats were summarized from Ellenberg *et al.* (1992). Taxonomic nomenclature followed Martinčič *et al.* (2007).

For each plot, we estimated in the field the following environmental variables: (1) micro-elevation (in cm) of the study plot above the present water line of the river (we roughly measured the elevation of the surface above the water line of the river using a tape measure); (2) relative presence of particular substrate categories: gravel, sand and silt (we visually estimated the approximate percentage of the substrate that corresponded to the texture size categories) and (3) bar age (1 = < 5 years, 2 = 5 to 10 years and 3 = > 10 years). The data for the approximate year of bar creation were obtained from aerial photographs and from personal communications.

Plant functional traits

In choosing key plant traits, we followed different literature sources (Hodgson *et al.,* 1999; Kahmen *et al.,* 2002; Cornelissen *et al.*, 2003). Information on plant species traits were chosen from our own database, from the literature (Martinčič *et al.,* 2007) and also from existing trait databases: BiolFlor (Klotz *et al.,* 2002, Kühn *et al.,* 2004), LEDA (Kleyer *et al.,* 2008), CLO-PLA (Klimešova & Klimeš, 2006; Klimešova & de Bello, 2009). We selected 10 traits for each species : "life form", "life cycle", "growth form", "plant height", "specific leaf area (SLA)", leaf dry matter content (LDMC)", "flowering start", "flowering end", "flowering period", "CSR strategy". The list of traits with the description of classes in the matrix and the sources of information are presented in Tab. 1. Categorical traits were all transformed into binary variables, with one for each possible level of the factor (dummy variables). In this way the number of traits in the matrix increased from 14 to 34 (Tab. 1).

Data Analysis

To analyse the gravel bar vegetation according to functional types composition, two data-matrix were composed: (a) species-relevé matrix (211 plant species x 143 relevés) and (b) a species-traits matrix (211 species x 34 plant traits). Braun-Blanquet cover-abundance data for the species were converted to a 2 to 9 scale (van der Maarel, 1979).

To determine the plant functional types, a species-traits matrix was subjected to divisive clustering, using WinTWINS version 2.3 (Hill & Šmilauer, 2005). Differences between plant functional types (Twinspan groups) were tested with Kruskal-Wallis test since the data were not normally distributed. Differences between groups were assessed using the Dunn-Bonferroni post hoc method.

In order to provide a visual representation of functional composition of mid-stream gravel bar vegetation, species names in the species-relevés matrix were replaced by plant functional types.

Plant functional types-environmental relationships were analysed using multivariate ordination techniques (Canoco for Windows, ter Braak & Šmilauer, 2002). Each vegetation record (relevé) was characterized according to the following features: i) environmental variables: substrate texture (gravel, sand and silt cover), height above water line (elevation), bar age (1 = < 5 years, 2 = 5 to 10 years and 3 = > 10 years), and ii)

Tab. 1: Plant traits, recorded on 211 vascular plant species from the river gravel bar vegetation along the Drava River in Slovenia. Scales of measurement were originally categorical or continuous.
Tab. 1: Morfološko-funkcionalne poteze za 211 rastlinskih vrst prodiščne vegetacije vzdolž srednjega toka reke Drave v Sloveniji. Podatki so bili v osnovi kategorični ali zvezni.

Traits	Abbreviation and description	Details	Data source
Life form	LF_Ha=chamaephytes; LF_Ge=geophytes; LF_He=hemicryptophytes; LF_Th=therophytes; LF_Ph=phanerophytes; LF_Hy=hydrophytes;	Categorical variable	Martinčič *et al.*, 2007
Life cycle	LC_Annu=annual; LC_Bien=biennial; LC_ Pere=perennial	Categorical variable	Martinčič *et al.*, 2007
Growth form	GF_Tuss= tussocks; GF_Rose = rosette; GF_le_st = leafy stem; GF_ro_le = rosette and leafy stem; GF_clem = climbers	Categorical variable	Rothmaler, 1995; Martinčič *et al.*, 2007
Plant height	P_height (cm)	Continuous variable	Own measurements
Specific leaf area	SLA (mm2/mg)	Continuous variable	Own measurements; LEDA database (Kleyer *et al.*, 2008)
Leaf dry matter content	LDMC (mg/g)	Continuous variable	Own measurements; LEDA database (Kleyer *et al.*, 2008)
Flowering start	F_start (month)	Continuous variable	Martinčič *et al.*, 2007
Flowering end	F_end (month)	Continuous variable	Martinčič *et al.*, 2007
Flowering period	F_lenght (months)	Continuous variable	Martinčič *et al.*, 2007
CSR strategy	C = competitors; S = stress-tolerators; R = ruderals	Categorical variable	Own measurements; Hodgson *et al.*, 1999

vegetation characteristics: number of plant species, vegetation cover and vegetation height. To relate functional composition to estimated environmental variables, Canonical Correspondence Analysis (CCA, ter Braak, 1986; Jongman *et al.*, 1995) was used. In CCA, vegetation characteristics were considered as supplementary environmental variables (in Canoco terminology). The values for herb layer cover (in %) and substrate texture (in %) were square-root transformed, whereas the elevation and vegetation height data were log(X + 1) - transformed prior to analysis. The effect of rare species was reduced by downweighting. The data were first subjected to Detrended Correspondence Analysis (DCA, Hill & Gauch, 1980). Gradient length for the first DCA axis was 3.385 SD (standard deviation) units, indicating that both types of ordination methods, linear and unimodal, were suitable for the analysis.

In the CCA, we applied manual forward selection (FS), mainly to see the sequence of contribution by individual variables to an explanation of species composition (Lepš & Šmilauer, 2003). The significance of each variable was evaluated using the Monte Carlo permutation test (499 permutations). Correlations between relevé scores of CCA axis 1 and environmental variables were analyzed using the Spearman rank-order correlation coefficient. All tests were performed with the statistical package SPSS Base ®for Windows 21.0 (Released in 2012, IBM, New York).

RESULTS AND DISCUSSION

In 143 plots (relevés) we identified 211 vascular plant species (mean = 17 ± 8 s.d. per relevé). The assemblage was strongly marked by species typical of disturbed habitats (56%), followed by species of riparian woodland/shrubland (14%), grassland species (11%), species of aquatic and wetland habitats and species with indifferent habitat preference (11% and 9%, respectively). Our results confirmed the relatively high floristic diversity that is typical of this landscape element, as has been described by other authors (Prach *et al.*, 1996; Gilvear & Willby, 2006). The position of passively projected environmental variables (number of plant species, vegetation cover and vegetation height) in the CCA indicated that the number of species in gravel bar vegetation increased with increasing gravel content, whereas vegetation cover and height increased with an increasing proportion of silt and sand (Fig. 2). It is likely that various soil properties, in particular substrate texture, are over-riding controls on gravel-bar plant species diversity.

Differences in functional composition were analyzed with TWINSPAN classification of the 211 species x 34 plant traits matrix (dendrogram not shown). Six clusters (groups FT1-FT6) emerged; the groups were defined as six main plant functional types (FT) of gravel bar vegetation (Tab. 2): (1) FT1 (33 plant species) includes mainly therophytes, pioneer ruderal species, characteristic for segetal plant communities from the class *Stellarietea mediae* such as *Amaranthus retroflexus, Capsella bursa-pastoris, Convolvulus arvensis, Conyza canadensis, Galinsoga parviflora* and *Sonchus oleraceus*. Species of FT1 are relatively small plants, with high SLA and low LDMC values (Tab. 2). They start to flower early in the season and have a long flowering period till the autumn; (2) FT2 (27 plant species) represents ruderal perennials, such as *Leersya orizoides, Lolium perenne, Myosoton aquaticum, Poa annua, Silene vulgaris* and *Tussilago farfara*; this plants are medium height and have high SLA values (Tab. 2); (3) FT3 (57 plant species) are hemicryptophytes with a substantial share of species from *Artemisietea vulgaris* class, such as *Artemisia vulgaris, Melilotus albus, Oenothera biennis,* and *Saponaria officinalis*; in comparison to FT2 (Tab. 2) these plant species are higher but with lower SLA values. Similar to FT1 they start with flowering earlier in the season; (4) FT4 (44 plant species) are late flowering annuals and biennials and when compared to annuals in FT1, species in FT4 are higher in growth and with higher LDMC values. Many of them are characteristic for hygrophilous ruderal vegetation of the class *Bidentetea tripartiti*, for example *Bidens tripartitus, Rorippa palustris, Xanthium italicum, Brassica nigra, Chenopodium ficifolium* and *Chenopodium album*; FT5 (30 plant species) are tall perennial herbs, with tussock growth form, such as *Barbarea stricta, Dactylis glomerata, Iris pseudacorus, Koeleria pyramidata, Molinia caerulea, M. arundinacea, Solidago gigantea* and *Urtica galeopsifolia;* FT6 (20 plant species) are phanerophytes, woody plant species with low SLA and high LDMC values (Tab. 2): their characteristic is also early and short flowering period. Species in FT6 are for instance *Acer campestre, Acer negundo, Populus alba, Populus nigra, Robinia pseudacacia, Salix alba, Salix caprea, Salix eleagnos, Salix fragilis, Salix purpurea, Salix triandra, Salix viminalis* and *Frangula alnus*. All defined FT are presented with 20 or more plant species (Tab.2). The highest number of plants is classified to FT3 (xerophilous ruderal perennials, N=57) and the lowest to FT6 (woody species, N=20). Functional groups represented by a larger number of plant species are typical for stable ecological systems. If one species goes extinct, another from the same FT can take place and the loss of one species will have less effect if others from the FT are preserved (Lawton & Brown, 1994).

In the CCA of all 143 vegetation relevés made on the gravel bars, species scores of axis 1 (eigenvalue=0.18) were positively correlated with silt cover ($R=0.52$, $p < 0.01$), vegetation cover and vegetation height ($R=0.6$, $p < 0.01$; $R=0.47$, $p < 0.01$, respectively), and negatively correlated with gravel cover ($R=-0.52$, $p < 0.01$), plot position above the water line ($R=-0.47$, $p < 0.01$),) and species number ($R=-0.24$, $p < 0.01$), as illustrated in Fig. 3.

In CCA analysis species names in the matrix species relevés were replaced by plant functional types in order

Tab. 2: Characteristics of six functional types (FT1-FT6) of plant species (N=211) of gravel bar vegetation (Middle Drava River, NE Slovenia). Legend: Numbers with different letters are significantly different at the 0.05 level.
Tab. 2: Značilnosti šestih funkcionalnih tipov (FT1-FT6) rastlinskih vrst (N=211) vegetacije prodišč srednjega toka reke Drave (SV Slovenija). Legenda: Vrednosti z različnimi črkami se statistično značilno razlikujejo pri p <0,05.

	FT1	FT2	FT3	FT4	FT5	FT6
Number of plant species	33	27	57	44	30	20
SLA (mm^2/mg)	$22.7±11^{ac}$	$37.8±18^{b}$	$23±7^{c}$	$20.2±7.3^{ac}$	$17.3±8.6^{a}$	$18.2±7.8^{ac}$
LDMC (mg/g)	$195.4±67.3^{a}$	$169.6±61.7^{a}$	$203.3±54^{a}$	$215.8±72.6^{a}$	$277.2±84^{b}$	$313.3±97.6^{b}$
Plant height (mm): mean ±s.d.	$341.5±259^{a}$	$374.2±241^{a}$	$463.2±225^{a}$	$481.6±268^{a}$	$526.5±359^{a}$	$7786.5±6967^{b}$
Flowering start (month)	$5.9±1.2^{b}$	$5.1±1.2^{ab}$	$5.9±1^{b}$	$6.5±0.9^{bc}$	$6.1±1.2^{b}$	$3.6±1.3^{a}$
Flowering end (month)	$9.4±1.2^{a}$	$8.3±1.4^{ed}$	$8.2±1.0^{bd}$	$8.9±0.8^{ae}$	$7.8±1.2^{bd}$	$5.1±1.5^{c}$
Flowering period (Number of months)	$4.6±1.6^{a}$	$4.1±1.2^{a}$	$3.3±0.8^{ad}$	$3.5±0.9^{d}$	$2.8±0.4^{bc}$	$2.5±0.8^{b}$

to relate functional composition of vegetation to environmental variables. The CCA analysis with 143 relevés made on the gravel bars and 211 plant species classified in six functional types (FT1-FT6) is shown in Fig. 2 for all FT-s together and in Fig. 3 a-c for separate pairs of FT-s. The arrangement of species in ordination indicated that plant functional diversity was highest on areas with higher proportion of gravel in soil, where all six FT could be found (Fig. 2) and where, from low to higher micro-elevations, FT1, FT2, FT3 and FT 4 were represented by larger number of species. Common to all four FT-s is functional traits characteristic for ruderal strategists (Grime, 2001): e.g. the tendency for the life-cycle to be that of the annual or short-lived perennial (FT1, FT4), high SLA (FT2) and low LDMC values (FT1-FT4) (Tab. 2). Plant functional types and traits are useful concepts to the understanding of the ecological processes of succession and competition (Duckworth *et al.,* 2000). Floods are the main disturbing factor on gravel bars and are fundamental in creating and maintaining gaps in vegetation. The bare ground conditions favor *pioneer* plant *species,* and periodic floods prevent total competitive displace-

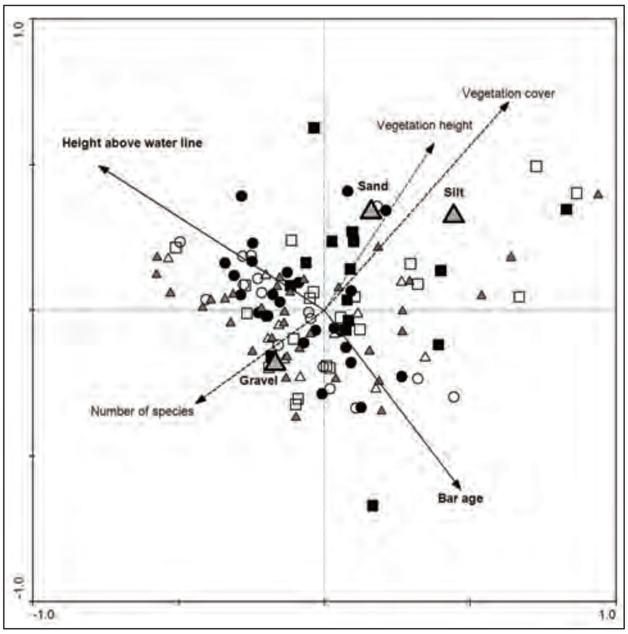
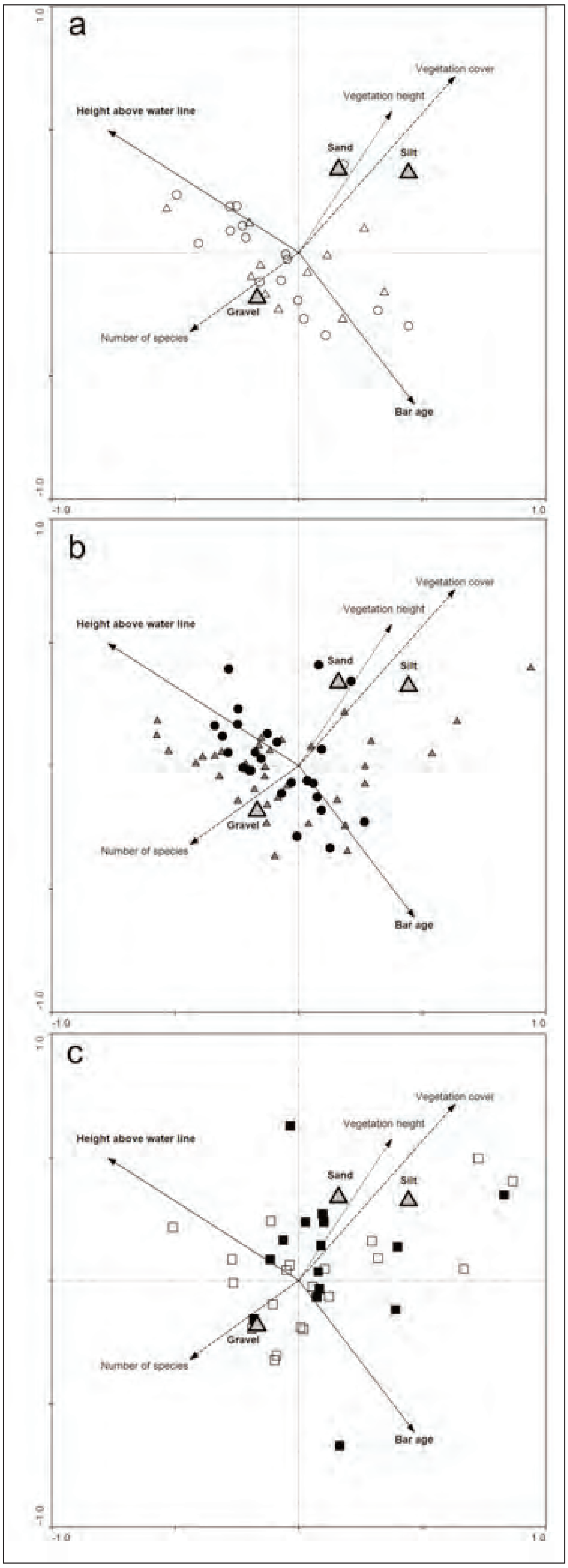


Fig. 2: CCA ordination diagram with environmental variables of river gravel bar vegetation (143 relevés) along the Drava River in Slovenia and plant species (N = 211) classified in six plant functional types (FT): FT1 = empty circle, FT2 = empty up-triangle; FT3 = gray up-triangle; FT4 = black circle; FT5 = empty square and FT6 = black square. Number of species, vegetation cover and vegetation height were added as supplementary variables (dashed line) without any affect on the analysis. Eigenvalues: 0.15 (axis 1), 0.14 (axis 2); 7.4 % of variance in species composition is explained by both axes.
Sl. 2: CCA ordinacijski diagram z okoljskimi spremenljivkami vegetacije prodišč (143 popisov) in rastlinskimi vrstami (N = 211), klasificiranimi v šest (6) funkcionalnih tipov (FT): FT1 = prazen krog), FT2 = prazen trikotnik), FT3 = siv trikotnik, FT4 = črn krog, FT5 = prazen kvadrat in FT6 = črn kvadrat. Število vrst, pokrovnost in višina vegetacije so v diagramu prikazane kot dodane spremenljivke (črtkana linija) brez vpliva na analizo. Lastne vrednosti osi: 0,15 (os 1), 0,14 (os 2). Prvi dve osi razložita 7,4 % variance v vrstni sestavi.



ment of pioneer species. Thus the functional types that usually are important (dominant) only in the early stages of succession will be present permanently in the mosaic vegetation of gravel bars. This pattern is consistent also with the intermediate-disturbance hypothesis (Gillison, 2016) as well as cyclic pattern of natural disturbance on gravel bar mosaics (e.g. gaps after periodic floods). Plant species form the FT2 and FT4 may be classified as competitive-ruderals, which occur in habitats of higher productivity in which dominance by competitors is prevented by disturbance. However, the sites colonised by competitive-ruderals experience a smaller effect of disturbance in comparison with areas populated exclusively by ruderals (Grime, 1977, 2001). Flowering in these plants is induced by increasing daylenght (summer annuals) preceded by a relatively long vegetative phase and at maturity, the shoots may be rather tall (e.g. *Impatiens glandulifera*). For the FT3 (thermophilous perennial) species centre of occurrence were areas on higher micro-elevations on gravel. They occupy habitats in which stress conditions, due to desiccation, could be experienced during the period of growth.

On the other hand, areas with silt/sand and on middle to high micro-elevation, were covered by dense vegetation and are characterized by lower number of plant species and lower functional diversity (Fig. 2). These substrates are usually moist and rich in available mineral nutrients and often support extremely rapid plant growth (van Dobben, 1967). In such conditions, the gravel bar vegetation was composed almost exclusively of FT5 (tall perennial herbs) and FT6 (woody plants) (Fig. 3a-3c).

Fig. 3: CCA ordination diagram with environmental variables of river gravel bar vegetation (143 relevés) along the Drava River in Slovenia and plant species (N=211) classified in: a) FT1 (empty circle) and FT2 (empty up--triangle); b) FT3 (gray triangle) and FT4 (black circle) and c) FT5 (empty square) and FT6 (black square). Number of species, vegetation cover and vegetation height were added as supplementary variables (dashed line) without any affect on the analysis. Eigenvalues: 0.15 (axis 1), 0.14 (axis 2); 7.4 % of variance in species composition is explained by both axes. Shown species have the highest weight.

Sl. 3: CCA ordinacijski diagram z okoljskimi spremenljivkami vegetacije prodišč (143 popisov) vzdolž srednjega toka reke Drave in rastlinskimi vrstami (N=211), klasificiranimi v: a) FT1 (prazen krog) in FT2 (prazen trikotnik); b) FT3 (siv trikotnik) in FT4 (črn krog) in c) FT5 (prazen kvadrat) in FT6 (črn kvadrat). Število vrst, pokrovnost in višina vegetacije so v diagramu prikazane kot dodane spremenljivke (črtkana linija) brez vpliva na analizo. Lastne vrednosti osi: 0,15 (os 1), 0,14 (os 2). Prvi dve osi razložita 7,4 % variance v vrstni sestavi. Prikazane so samo vrste (kot funkcionalni tipi), ki imajo največjo obtežbo v analizi.

Combination of characteristic plant functional attributes in FT5 and FT6 (e.g. tall stature) suggested that competition is the key factor process which affects the structure of trait values within these habitats. Gravel bars are usually poor in nutrients and their vegetation full of gaps, where there is no competition between plants. Nutrient availability increases in gravel bars that are impacted by reduced hydrodynamics (Müller & Okuda, 1998).

CONCLUSIONS

We investigated the functional composition of gravel bar vegetation using plant functional traits and environmental properties. Our analysis of the species-traits data resulted in six plant functional types which may coexist within gravel bar plant communities. Conditions of intermediate fertility and disturbance (areas with coarse gravel sediments, from low to higher micro-elevations) promote coexistence of a greater diversity of species and functional types (strategies) (Grime, 2001). More fertile and moist conditions on areas with fine silt and sand sediments increased the dominance by tall plants with more competitive strategies, thereby leading to lower species richness and lower number of plant functional types. Complementarity between functional groups may have important consequences for conservation planning at landscape scale. Where clear evidence indicates that the number of different functional groups increases with number of species, as we observed in our study, conserving a large proportion of the plant functional traits will also require conserving a large proportion of all species (Petchey & Gaston, 2002). Unfortunately, the natural floodplain dynamics and diverse riparian landscape of most gravel-bed rivers in Europe are under enormous anthropogenic pressure, in the form of canalization, gravel exploitation and flood control measures. This study also shows that gravel bars form a highly significant landscape element (component) in terms of maintaining higher species and *functional diversity* of the middle Drava river ecosystem.

FUNKCIONALNA SESTAVA VEGETACIJE PRODIŠČ SREDNJEGA TOKA REKE DRAVE (SV SLOVENIJA)

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POVZETEK

Z raziskavo na prodiščih srednjega toka reke Drave v Sloveniji smo z vzorčenjem vegetacije, ob upoštevanju morfološko-funkcionalnih potez rastlin in okoljskih dejavnikov, ugotavljali funkcionalno sestavo prodiščne vegetacije. Prodišča predstavljajo prehodno območje med vodnim in kopenskim ekosistemom, kar omogoča razvoj različnih habitatov in je zaradi številnih okoljskih dejavnikov in procesov značilna vegetacijska dinamika. Biodiverziteta prodišč je zato lahko zelo visoka. Funkcionalna sestava kot komponenta biodiverzitete ima bistveno vlogo pri številnih ekosistemskih funkcijah, zato so raziskave funkcionalne pestrosti nujne za celostno poznavanje in razumevanje delovanja ekosistemov. Na območju srednjega toka reke Drave med Ptujem in Ormožem smo vzorčili vegetacijo po standardni srednjeevropski fitocenološki metodi na 143 popisnih ploskvah. Na vsaki ploskvici smo zbrali podatke o naslednjih okoljskih dejavnikih: višini popisne ploskvice nad gladino vode (v cm), deležih proda, peska in mulja (v %) ter starosti prodišča. Popisali smo 211 vrst oz. taksonov rastlin, za katere smo zbrali tudi podatke o 10 morfološko-funkcionalnih potezah (MFP). Podatke smo analizirali s klasifikacijskimi in ordinacijskimi metodami. S Twinspan analizo smo razvrstili vrste na osnovi MFP v šest funkcionalnih tipov (FT). Na osnovi ordinacijskih analiz smo ugotavljali povezavo med merjenimi okoljskimi dejavniki in pestrostjo FT. Ugotovili smo, da je najvišja pestrost vrst, in tudi FT, na tistih delih prodišč, kjer je največji delež prodnate podlage, saj so se tam pojavljale vrste vseh šestih FT. Takšna tla so zmerno hranljiva in podvržena zmerni motnji (poplavam), kar omogoča sobivanje večjega števila vrst in funkcionalnih tipov. Na območjih prodišč, kjer so tla bogatejša s hranili in vlažna (mesta, kjer v tleh prevladujeta mulj in pesek), se uveljavijo in prevladujejo rastlinske vrste z bolj kompetitivnimi strategijami, kar vodi v manjšo pestrost vrst in manjše število funkcionalnih tipov. Na predelih prodišč z zmernimi okoljskimi razmerami smo ugotovili komplementarnost funkcionalnih tipov v vegetaciji, kar ima zelo pomembno uporabno vrednost pri načrtovanju ustreznega upravljanja s temi habitati za njihovo ohranjanje. Kadar z naraščanjem števila vrst narašča funkcionalna pestrost, kot smo ugotovili v raziskavi, je pogoj za ohranitev obstoječih funkcij ekosistema ohranitev velikega števila prisotnih vrst. Z raziskavo smo še potrdili, da so prodišča pomemben element rečne krajine, saj značilno prispevajo k raznolikosti vrst in ekoloških funkcij v rečnem ekosistemu.

Ključne besede: Funkcionalne poteze rastlin, funkcionalna pestrost, rečni ekosistemi, rastlinska pestrost, poplavna motnja, Natura 2000.

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